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Interactions of predominant insects and diseases with climate change in Douglas-fir forests of western Oregon and Washington, U.S.A.

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ABSTRACT

Forest disturbance regimes are beginning to show evidence of climate-mediated changes, such as increasing severity of droughts and insect outbreaks. We review the major insects and pathogens affecting the disturbance regime for coastal Douglas-fir forests in western Oregon and Washington State, USA, and ask how future climate changes may influence their role in disturbance ecology. Although the physiological constraints of light, temperature, and moisture largely control tree growth, episodic and chronic disturbances interacting with biological factors have substantial impacts on the structure and functioning of forest ecosystems in this region. Understanding insect and disease interactions is critical to predicting forest response to climate change and the consequences for ecosystem services, such as timber, clean water, fish and wildlife. We focused on future predictions for warmer wetter winters, hotter drier summers, and elevated atmospheric CO_2 to hypothesize the response of Douglas-fir forests to the major insects and diseases influencing this forest type: Douglas-fir beetle, Swiss needle cast, black stain root disease, and laminated root rot. We hypothesize that (1) Douglas-fir beetle and black stain root disease could become more prevalent with increasing, fire, temperature stress, and moisture stress, (2) future impacts of Swiss needle cast are difficult to predict due to uncertainties in May-July leaf wetness, but warmer winters could contribute to intensification at higher elevations, and (3) laminated root rot will be influenced primarily by forest management, rather than climatic change. Furthermore, these biotic disturbance agents interact in complex ways that are poorly understood. Consequently, to inform management decisions, insect and disease influences on disturbance regimes must be characterized specifically by forest type and region in order to accurately capture these interactions in light of future climate-mediated changes.

1. Introduction

Disturbance regimes in forests of western North America are showing evidence of climate-mediated shifts associated with global climate change in the form of historically unprecedented tree mortality (Anderegg et al., 2012; van Mantgem et al., 2009). Instigating factors for these mortality events include extreme drought (Allen et al., 2015; Asner et al., 2015), increased fire severity and extent (Abatzoglou and Williams, 2016), and expansion of bark beetles into previously climatically unsuitable habitat (Bentz et al., 2010; Björkman and Niemelä 2015). The frequency and severity of forest disturbances will likely continue to increase given predicted climate-related changes in environmental conditions over the 21 st century (Allen et al., 2015), which will influence a range of characteristics of these forests including the ecosystem services that they provide (Johnstone et al., 2016; Seidl et al., 2016).

Projected changes in climate will make forests more vulnerable to tree mortality resulting from physiological stress interacting with other climate-influenced events, such as insect and disease outbreaks, droughts and fires (Beedlow et al., 2013; Kolb et al., 2016; Weed et al., 2013). Current predictions for major climate-related trends affecting forests in western North America include increased fire season length and burned area (Abatzoglou and Williams, 2016; Flannigan et al., 2013), increased occurrence of severe drought (Allen et al., 2015), reduced mountain snowpack (Kapnick and Hall, 2012), and generally increasing temperature, with seasonal trends including warmer wetter winters, and hotter drier growing seasons (Rupp et al., 2016).

There is a growing interest in understanding the interactions of

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multiple disturbance factors (Anderegg et al., 2015; Johnstone et al., 2016; Law and Waring, 2015) in forest ecosystems because their combined effects can differ from that of any single agent acting alone (Seidl et al., 2016). However, interactions for any given forest type vary by landscape character, forest structure, specific insect herbivores and forest pathogens, as well as seasonal climatic factors, storms, and fire patterns. Consequently, to inform management decisions, disturbance regimes must be characterized specifically by forest type and region in order to accurately capture these interactions and allow for prediction of future climate-mediated changes. If conducted at a scale at which management actions are implemented, such as forests with the same dominant tree species and climatic conditions, assessments of potential climate-related changes to disturbance regimes can greatly improve our ability to adaptively manage our forests and the ecosystem services they provide.

Here, we examine the primary insects and diseases (referred to throughout as biotic disturbance agents) of Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco). Although western hemlock is commonly found as a co-dominant in Douglas-fir forests, especially in old growth forests, Douglas-fir is the dominant species on most of the forested land from near sea-level to roughly 1200 m elevation in western Oregon and Washington, U.S.A. Further, Douglas-fir is the principle timber species, and it is ecologically important for carbon sequestration, and wildlife habitat, as well as being vital for the production of hydropower, irrigation, and drinking water (Curtis and Carey, 1996; Harmon et al., 2004; Kline et al., 2016; Ruggiero et al., 1991). Ecological effects of the major disturbance regimes, especially fire and logging, have been studied extensively in this forest type (Cohen et al., 2002; Creutzburg et al., 2016; Healey et al., 2008; Tepley et al., 2013; Wimberly and Spies, 2001). However, the role of insects and diseases within the disturbance regime has not been adequately addressed, even though there is currently a major foliage disease (Swiss needle cast) epidemic occurring in the region (Ritóková et al., 2016).

Here, we: (1) identify the impacts of the major insects and diseases affecting Douglas-fir and their interactions, (2) integrate our understanding of temperature and moisture stress in trees with future climate projections to hypothesize changes in disturbance agent behavior under climate change, and (3) highlight important knowledge gaps in the understanding of the current and projected disturbance regimes in coastal Douglas-fir forests.

2. Ecological setting

Coastal Douglas-fir forests extend from British Columbia through northwestern California. However, we constrain the geographical extent to Washington and Oregon, west of the crest of the Cascade Mountain Range where Douglas-fir is the dominant tree species (Fig. 1), which has traditionally been called the “Douglas-fir region” (Franklin, 1979; Jensen, 1955). This is a moist temperate forest region is dominated by conifers and has relatively long time periods between high severity natural disturbances (Franklin, 1979). The climate is characterized by mild, wet winters, lack of soil freezing, most precipitation falling as rain, a summer drought, and a strong influence from large-scale oscillations such as the El Niño-Southern Oscillation (ENSO), the Pacific North American pattern, and the Pacific Decadal Oscillation (PDO) (Abatzoglou et al., 2014; Dalton et al., 2013). Douglas-fir forests are some of the most productive in the world, with biomass accumulations far exceeding those of both tropical and other northern temperate forests (Law and Waring, 2015; Waring and Franklin, 1979). The large biomass accumulation results from the sustained height growth, foliage retention, and longevity of the dominant trees rather than from high annual net productivity (Waring and Franklin, 1979).

Douglas-fir forests span multiple ecoregions (Fig. 1A) and are generally found within the *Picea sitchensis* and *Tsuga heterophylla* zones, with some of their range in the *Abies amabilis* zone (Franklin, 1979; Franklin and Dyrness, 1988), and generally correspond to the Maritime Coniferous Forests of the Pacific Northwest, U.S.A. (Peterson et al., 2014). Depending on geographic location and stand history, the predominant tree species is Douglas-fir (Franklin and Dyrness, 1988). Douglas-fir comprises approximately 77% of saw timber stumpage volume in western Washington and Oregon (Howard, 2007), as well as 50% of aboveground carbon storage in Oregon (Donnegan et al., 2008). These forests often contain variable proportions of western hemlock (*Tsuga heterophylla* [Raf.] Sarg.), Sitka spruce (*Picea sitchensis* [Bong.] Carrière), western redcedar (*Thuja plicata* Donn ex D. Don), and grand fir (*Abies grandis* [Douglas ex D. Don] Lindley) at lower elevations, while Pacific silver fir (*A. amabilis* Douglas ex J. Forbes) and noble fir (*A. procera* Rehder) can be found at higher elevations.

The region includes a range of topographical features and environmental conditions. The productivity and survival of trees in these forests can be influenced by various limiting factors related to climate. Although nutrients can have substantial influence on productivity and survival, forests are typically either water-limited or energy-limited (Beedlow et al., 2013; Littell et al., 2010). Within this region, water limitation may result from either reduced precipitation (Bumbaco and Mote, 2010), a reduction of winter snowpack which normally provides water to lower elevation forests during a growing season (Albright and Peterson, 2013), or excessively well-drained soils (Littell et al., 2008). Energy limitation primarily involves light availability (Beedlow et al., 2013) but can involve temperature, particularly in the case of higher-elevation forests with decreased growing seasons due to lower temperatures (Littell et al., 2008). Light is often limited due to cloud cover or dense forest conditions leading to low light availability and reduced photosynthesis (Runyon et al., 1994).

Contemporary climate trends are apparent in the region. Annual mean temperature increased by approximately 0.7–0.9 °C from 1901 to 2012; other climate trends in the region include a lengthened freeze-free season, increased temperature of the coldest night of the year, and increased growing-season potential evapotranspiration (Abatzoglou et al., 2014). Warming has led to approximately a 20% loss of winter snowpack since 1950 (Mote, 2006), while spring snowmelt has occurred up to 30 days earlier depending on location (Stewart et al., 2005). Observations show a long-term increase in spring precipitation, but decreased summer and autumn precipitation and increased potential evapotranspiration have resulted in larger climatic water deficits over the past four decades (Abatzoglou et al., 2014).

The natural disturbance regime of the region is driven by long-term forest succession with local patch-scale dynamics, followed by stand replacement fire (Franklin et al., 2002). Large-scale disturbances prior to European settlement resulted primarily from marine-generated windstorms and wildfire, while volcanic eruptions, floods and landslides were less common (Franklin et al., 2002, 2017). However, the disturbance regime has been altered. Throughout much of this forest type, the primary disturbance is now forest management (Berner et al., 2017; Cohen et al., 2002). Berner et al. (2017) estimated that in Oregon and Washington, timber harvesting resulted in ~80% of observed tree mortality from 2003 to 2012.

With the exception of wilderness and other protected areas, forest management is pervasive throughout the Douglas-fir region. For this reason, forest management provides a backdrop for understanding the interactions with biotic disturbance agents affecting these forests. The long-term effect of timber harvesting has been a regional shift from old to young forests. Old growth forests (250+ years) occupied around half of the forested area before industrial logging (Franklin et al., 2017). Currently, 41% of the region that is forested is occupied by trees aged under 50 years and 7% of the forested region is greater than 250 years old (Fig. 2).

We define forest management as active management (i.e., road construction, logging, prescribed fire, replanting, understory vegetation management), but the magnitude of the disturbance created by forest management is nonetheless highly variable. For example, public lands (federal, state and local), which occupy 50.8% of the region (Fig. 3), tend

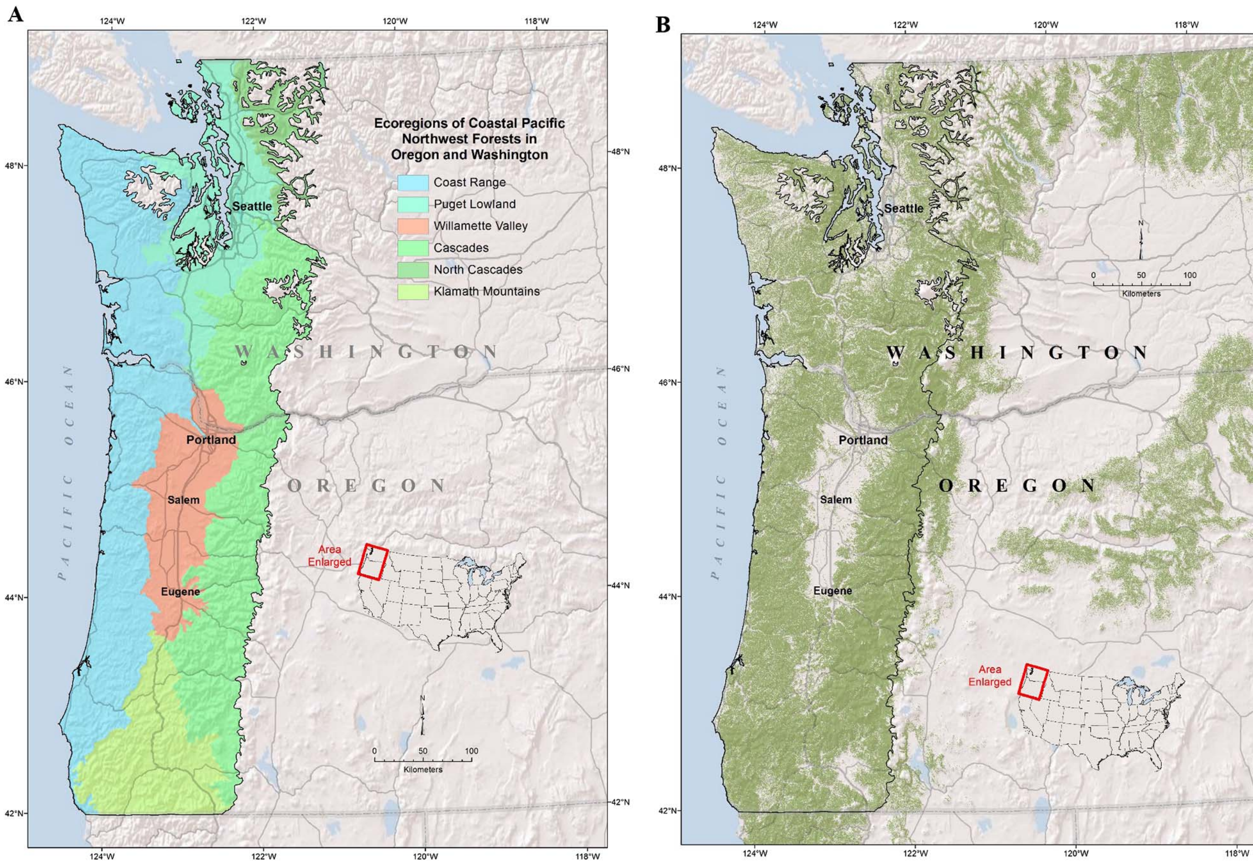

Fig. 1. Extent of coastal Pacific Northwest Douglas-fir forests in Oregon and Washington based on aggregated Level IV Ecoregions where Douglas-fir is described as the dominant species. (A) Level III Ecoregion designations: Coast Range (40,922 km^2, 32%), Puget Lowland (16,970 km^2, 13%), Willamette Valley (14,885 km^2, 12%), Cascades (34,972 km^2, 27%), North Cascades (5165 km^2, 4%), Klamath Mountains (15,579 km^2, 12%). (Source: Level III and IV ecoregions of the continental United States: Corvallis, Oregon, U.S. EPA – National Health and Environmental Effects Research Laboratory, map scale 1:7,500,000, https://www.epa.gov/eco-research/level-iii-and-iv-ecoregions-continental-united-states). (B) Occurrence of Douglas-fir (*Pseudotsuga menziesii*) in the Pacific Northwest region of the United States (Washington/Oregon study region outlined in black). (Source: GNN maps for Washington, Oregon, and California, 2012, https://lemma.forestry.oregonstate.edu/data/download/?file=/export/grids/sppsz/r2/gnn_sppsz_2014_08_28.zip).

to be managed for multiple uses, rather than optimized solely for timber production. Public lands contain the majority of older forests (Fig. 2), including late-successional forests (Creutzburg et al., 2016; Forest Ecosystem Management Assessment Team, 1993). There is much variation in management actions on public lands where variable retention harvest, which retains standing live or dead trees or live patches within cut areas, is common, and natural regeneration may be preferred to planting (Franklin and Johnson, 2012). Timber harvests may also take the form of thinning in forests where the goal is to increase structural complexity, rather than to maximize timber outputs (Bailey and Tappeiner, 1998; Thomas et al., 2006), although thinning treatment effects are highly variable and site-dependent (Puettmann et al., 2016).

Nearly half of the land area in Douglas-fir region exists on private land (Fig. 3) on which management practices represent a disturbance of much higher intensity. Industrial land in this region typically consists of single-aged monocultures of Douglas-fir on a rotation of under 50 years—69% of forests < 50 years old are privately owned (Fig. 2). Plantation forests generally lack coarse woody debris, snags, and live residual trees from the previous stand, while non-crop vegetation is controlled (Franklin et al., 2002). Clearcuts are favored over thinning (Ohmann et al., 2007), and tree seedlings grown from improved genetic stock are typical in replanting. Intensive management includes interventions such as herbicide use and burning to control early seral vegetation to ensure planted seedlings or saplings establish successfully (Curtis et al., 2007). Thus, the early seral stage of this forest type is often avoided and stages which favor establishment of overstory trees occur quickly after stand establishment (Ohmann et al., 2007; Swanson et al., 2011, 2014).

The interaction of forest management and fire is complex and varies across the region. While the legacy of fire suppression has decreased the area burned in some Douglas-fir forests since 1950, particularly in more xeric areas (Weisberg and Swanson, 2003), this practice has not influenced Douglas-fir forests to the same degree as it has other forest types in the western US (Brown et al., 2004; Mitchell et al., 2009). Creutzburg et al. (2016) suggest that intensive forest management may contribute to decreased fire activity in this forest type. Conversely, Thompson et al. (2007) noted that in more xeric areas, fire severity increased in stands that had been previously salvage-logged and planted, suggesting that although surface fuels were reduced, a continuous canopy fuel layer was promoted.

3. Physiological response to water and temperature stress

The proximate effects of climate change on Douglas-fir forests are increased temperature and water stress, particularly during the summer drought. However, they interact with insect pests and diseases to affect tree mortality. Here, we present the basic physiological effects of water and temperature stress in trees to better understand the interactions of biotic disturbance agents within a forest context. Water stress typically appears first in trees growing on sites with features such as south-facing slopes, shallow soils, convexities on slopes, and ridgetops, then spreads to less vulnerable sites as the drought intensifies (Western et al., 1999). Water availability influences a range of important physiological processes within plants including stomatal conductance, photosynthesis, cell division, cell expansion, phloem transport, nutrient transport and metabolic function (Hsiao, 1973). When sufficiently severe, water

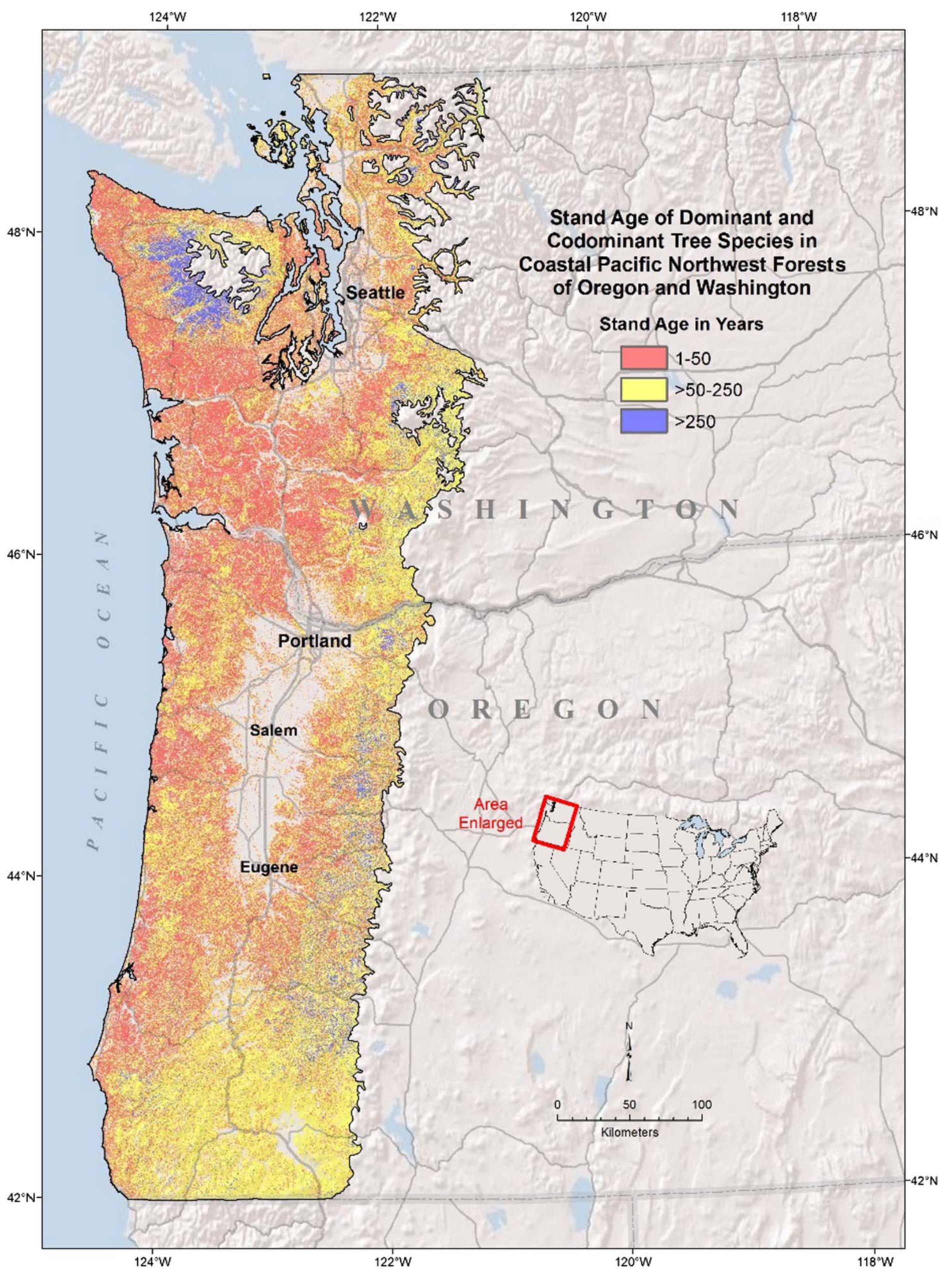

Fig. 2. Stand age classes in the Douglas-fir region. Color codes indicate three age classes for dominant and co-dominant tree species; red = 1–50 year-old stands (4.12 million ha, 41%), yellow = 50–250 year-old stands (5.34 million ha, 53%), and blue ≥250 years old (0.67 million ha, 7%). Young forests are the predominant age class across the region, which is 59% forested. (Source: GNN maps for Washington, Oregon, and California, 2012, https://lemma.forestry.oregonstate.edu/data/download/?file=/export/grids/sppsz/r2/gnn_sppsz_2014_08_28.zip). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

deficit can also lead to loss of leaf area, the disruption of the soil-to-leaf hydraulic continuum, the inhibition of seedling germination, dead tops, branch flagging, foliage loss, wilting, chlorosis, and whole tree mortality (Breda et al., 2006; Goheen and Willhite, 2006). These symptoms are most common in smaller trees, while larger water-stressed trees may not show visual damage (Lavender and Hermann, 2014). Various root, bole, branch, bark and tip insects and pathogens are associated with water-stressed trees (Goheen and Willhite, 2006).

Elevated temperatures can cause an array of biochemical and physiological effects in plants that negatively influence plant growth and development (Bray et al., 2000). Temperature plays a fundamental role in plant-water relations because as air temperature increases, it is able to hold more water. The difference between the amount of moisture in the air and how much moisture the air can hold when it is saturated is the vapor pressure deficit (VPD). Increasing VPD creates drier conditions for plants by drawing more water out of the soil and plant tissues via increased evaporation and transpiration. In water-limited ecosystems, these effects may lead to substantial reductions in ecosystem productivity. High temperature can also inhibit seed germination and at later developmental stages it can affect respiration, photosynthesis, and water relations (Wahid et al., 2007). In general, photosynthetic rates decrease under high temperatures (Bernacchi et al., 2001), while dark- and photo-respiration rates increase (Raich and Schlesinger, 1992). However, some research has shown an overall enhancement of growth under moderately increased temperature in some ecosystem types (Way and Oren, 2010).

In western Oregon, a primary climatic factor limiting Douglas-fir growth is VPD (Beedlow et al., 2013; Lee et al., 2016). Aridity can both reduce soil water availability and increase VPD. Therefore, drought can negatively impact stomatal conductance and photosynthesis on both ends of the soil-to-leaf hydraulic continuum (Bond and Kavanagh, 1999; Domec et al., 2004; Kavanagh et al., 1999). The reduction in soil water availability reduces soil water potential, leading to a reduction in the difference in water potential between the soil and the leaves, which represents the driving force for xylem water transport. As soil water potential declines, either leaf water potential must decline to maintain a

Fig. 3. Distribution of land ownership in the Douglas-fir region. Area (% of forested land) in the Douglas-fir region under: Private management = 5.20 million ha (49.2%), Federal management = 4.35 million ha (41.1%), State and local management = 1.02 million ha (9.7%). (Source: U.S. Geological Survey, Gap Analysis Program (GAP). May 2016. Protected Areas Database of the United States (PAD-US), version 1.4 Combined Feature Class.)

sufficient driving force or xylem water transport declines. Once leaf water potential decreases to a threshold level, stomatal closure occurs until leaf water potential is able to sufficiently recover. If leaf water potential becomes too great, this tension within a plant's hydraulic pathway can create air bubbles (emboli) that block water transport in the water conducting xylem tissue of the plant. These emboli can be repaired when conditions allow xylem cells to be refilled with water, but if conditions do not allow repair then foliage may become desiccated, potentially leading to plant death. In addition, drought effects on Douglas-fir, and the mechanisms by which they withstand drought, vary with tree age. For example, Phillips et al. (2003) used sap flux measurements in young and old Douglas-fir trees to show that older, larger trees rely substantially more on stored water than younger trees, with water stored in xylem accounting for 7% of daily water use in young (15 m) trees, and 20–25% in older (60 m) trees.

When transpiration is reduced by stomatal closure, the hydraulic system of the plant is protected, to a degree. However, this comes at the cost of cessation of carbon assimilation because stomatal conductance controls both water vapor leaving the plant and CO_2 entering the plant (Buckley 2005). Stomatal closure can lead to reductions in carbohydrate reserves because metabolic consumption of reserves continues despite the interruption of photosynthesis. If drought or high VPD conditions persist, prolonged periods of stomatal closure can potentially lead to the depletion of available non-structural carbohydrates and to reduced annual growth (Sala et al. 2012). Separating the confounding effects of water and temperature stress on annual growth is difficult because climate variables are highly correlated and interact in various ways depending upon site conditions. Other seasonal climatic and biotic disturbance factors may also have indirect effects on growth by reducing photosynthesis, damaging plant tissue, or impairing physiological processes (e.g., Lee et al., 2013, 2016).

4. Biotic disturbance agents

Disturbance dynamics vary widely among Douglas-fir forests by structure and age. We focus on the insects and pathogens, which

Table 1
Major insects and diseases of Coastal Pacific Northwest Douglas-fir, their influences on tree physiology, stand impacts, and interactions under current climate conditions.

Biotic agent	Physiological influences	Stand impacts	Disturbance interactions
Laminated root rot (*Phellinus sulphurascens)*	Increased water stress due to root mortality	Reduced tree growth, mortality	Douglas-fir beetle associated with laminated root rot, exacerbated by management
Black stain root disease (*Leptographium wagneri)*	Reduced stem hydraulic conductivity	Reduced tree growth, mortality	Increases with drought, insect vector activity, and forest management
Swiss needle cast (*Phaeocryptopus gaeumannii)*	Reduced photosynthesis due to blockage of stomata	Reduced tree growth	Exacerbated by management. Reduced Douglas-fir beetle, reduced dominance of Douglas-fir
Douglas-fir beetle (*Dendroctonus pseudotsugae)*	Tree death, reduced phloem and xylem transport due to gallery development and introduction of stain fungi	Reduced tree growth, mortality	Increases with laminated root rot, decreases with Swiss needle cast, increases with drought, associated with major windthrow events

interacting with temperature and moisture stress commonly result in climate-related tree mortality within the region. These include laminated root rot (caused by *Phellinus sulphurascens* [Pilat]), black stain root disease (caused by *Leptographium wagneri* [Kendrick] Wingfield), Swiss needle cast (caused by *Phaeocryptopus gaeumannii* [Rohde] Petrak), and Douglas-fir beetle (*Dendroctonus pseudotsugae* Hopkins, Coleoptera: Curculionidae: Scolytinae). These are all biologically mediated factors, which interact with forest management, fire, and extreme weather events—the major forest disturbances in the region (Table 1). Because the intent of this paper is to highlight biotic disturbance agents we do not address disturbance types separately, but rather discuss them in conjunction with specific biotic agents. Disturbances not affected by climate, such as volcanism and earthquakes are not considered here even though they may subsequently affect biotic factors such as bark beetles.

4.1. Laminated root rot

Laminated root rot, caused by the fungal pathogen *Phellinus sulphurascens*, is a localized and persistent disease of most tree species in the Douglas-fir region. It survives in tree stumps and woody roots in the soil, grows clonally on roots, and rarely spreads by spores (Hansen and Goheen, 2000; Lockman and Kearns, 2016). *Phellinus sulphurascens* is a native pathogen that can kill trees of any age or vigor, and is estimated to be present in 5–13% of the forest stands in the region (Washington Academy of Sciences, 2013). The effects of laminated root rot vary with stand composition and management actions. In intensively managed plantation forests, a decrease in volume production of about 25% is associated with this disease (Thies and Westlind, 2005), resulting in a substantial economic loss. The continual planting of trees in plantations on diseased sites enhances the spread and enlargement of the area infested. In forests managed with lower intensity, laminated root rot is controlled by low host density, root tip-ups which pull wood out of the soil, and is associated with canopy gap creation, structural diversity, and increased abundance of non-host tree species (Hansen and Goheen, 2000; Thies and Sturrock, 1995), characteristics which may be favorable for ecological management (Franklin et al., 2002).

Estimated annual timber losses in Washington associated with laminated root rot in Douglas-fir are 0.9 million m^3 (Washington State Academy of Sciences, 2013). Although this volume loss indicates a large decrease in carbon sequestration in these forests, carbon storage gains in non-infected trees following gap creation have not been quantified (Hansen and Goheen, 2000), so the carbon dynamics associated with this disease are not straightforward. Additionally, carbon is retained in decaying material for many years (Harmon et al., 2004). This decaying material also allows *P. sulphurascens* to remain on a site for up to 50 years (Hansen and Goheen, 2000), so replanting where trees have been killed by *P. sulphurascens* leads to inoculum buildup and substantial decreases in site productivity over time (Nelson et al., 1981).

Phellinus sulphurascens spreads through root to root contact via ectotrophic mycelia, penetrating the host's roots and killing the phloem and cambium, while decay occurs in the xylem (Hansen and Goheen, 2000). Sexual reproduction is rare therefore the pathogen spreads vegetatively at an estimated rate of about 30 cm (cm) per year depending on stand age and composition. However, given the long residence time of the inoculum and abundance of hosts on the landscape, it is likely that disease is slowly increasing because current forest management practices result in continual availability of susceptible Douglas-fir.

4.2. Black stain root disease

Black stain root disease is another apparently native root disease that occurs on Douglas-fir (Lockman and Kearns, 2016). It is caused by the fungal pathogen *Leptographium wageneri* (Hessburg et al., 1995) and is vectored primarily by the root-feeding bark beetle, *Hylastes nigrinus* (Mann.) (Coleoptera: Curculionidae: Scolytinae) and the reproduction weevils *Pissodes fasciatus* LeConte (Coleoptera: Curculionidae) and *Steremnius carinatus* (Boheman) (Coleoptera: Curculionidae) (Witcosky and Hansen, 1985; Witcosky et al., 1986). In Douglas-fir the disease is most damaging in young trees and is most commonly found in plantations under 30 years of age (Hansen and Goheen, 1988). Infection is associated with stressed trees, wounding, and stump creation during precommercial thinning (Harrington et al., 1983; Hessburg and Hansen, 2000), likely due to the release of ethanol by host trees or recently created stumps, which attracts the insect vectors (Kelsey and Joseph, 1998).

Black stain root disease spreads via root grafting with neighboring hosts as well as by insect vectors (Hessburg et al., 1995). Transmission via grafting may cause disease centers to expand at about 0.8–1.5 m per year. Disease spreads more rapidly in time and space via insect vectors, notably by the bark beetle *Hylastes nigrinus* that is capable of flight. These insects vector the pathogen by transporting spores and increase host susceptibility to infection by damaging roots as adults in feeding attacks or as larvae developing in the host (Witcosky and Hansen, 1985). Infection with *L. wageneri* further attracts pathogen-vectoring insects by host signaling via ethanol production, resulting in a positive feedback loop once trees are infected (Kelsey and Joseph, 1998). Ethanol production also increases when trees are water-stressed, so this disease is likely to be most severe during episodic droughts and on xeric sites.

Leptographium wageneri colonizes the sapwood xylem in the roots, which blocks water transport to the upper stem and foliage, eventually killing the tree (Hessburg et al., 1995). The fungus requires wounding to enter the xylem, thus it appears fine root mortality leads to increased infection point availability (Hessburg and Hansen, 2000). Fine root mortality is caused by many factors including water-stress, insect attacks, fungal infection, and foliage loss (Hessburg and Hansen, 2000), so increases in any of these factors could increase the prevalence of this disease. Forest management also influences black stain root disease and its vectors directly by creating stumps in clearcuts and thinned stands, wounding trees in thinning operations and along roadsides, and where soils are compacted (Harrington et al., 1983; Hessburg et al., 1995; Witcosky and Hansen, 1985). We hypothesize that intensification of short rotation forest management on the landscape will increase black

stain root disease by providing more suitable habitat in monocultures of young Douglas-fir, increasing occurrence of stumps, and increased vector beetle populations.

4.3. Swiss needle cast

Swiss needle cast is a foliage disease specific to Douglas-fir. It is endemic throughout the range of the host species, although economically, it is of most concern in coastal plantations. Caused by the endophyte fungal pathogen *Phaeocryptopus gaeumannii*, the disease develops when fruiting bodies (pseudothecia) form within the stomata of the needles, limiting carbon uptake and photosynthesis (Manter et al., 2005). As stomata are plugged, needles become chlorotic and are eventually abscised (Hansen et al., 2000), leading to up to a 50% loss in stem volume growth in the most severely infected hosts (Maguire et al., 2011). Douglas-fir forests in the coastal Pacific Northwest have been experiencing a Swiss needle cast epidemic since 1990 (Hansen et al., 2000), and the area with symptomatic trees has increased dramatically over the last two decades (Ritóková et al., 2016). The area affected in coastal Oregon has increased from 53,000 ha in 1996 to 221,000 ha in 2016 (Swiss Needle Cast Cooperative, 2017). Over 100,000 ha of affected area was mapped in 2016 in western Washington (Swiss Needle Cast Cooperative, 2017). Although this native pathogen was present in this region prior to 1990, its effects were endemic, while impacts since 1990 have represented an increasingly important concern for management (Hansen et al., 2000; Ritóková et al., 2016).

Changes to forest management, climate change, or a combination of these have been implicated as catalysts for the current Swiss needle cast epidemic. Disease impacts are most notable in the *Picea sitchensis* zone and low elevation regions near the coast, where Douglas-fir was not historically found at the densities that it is planted in current intensive forest management practices (Black et al., 2010; Hansen et al., 2000; Manter et al., 2005). This region also has naturally high levels of soil nitrogen, which correlate with disease expression, although the presence of a causal relationship is equivocal (Perakis et al., 2005). However, Swiss needle cast has intensified beyond the coastal strip to about 50 km inland in some areas (Ritóková et al., 2016). Warm winter temperatures and leaf wetness during spore dispersal in late spring and summer are associated with increased Swiss needle cast severity (Black et al., 2010; Lee et al., 2013; Manter et al., 2005; Rosso and Hansen, 2003; Stone et al., 2008). Various specific metrics have been shown to influence disease severity including December to February temperature and summer leaf wetness (Manter et al., 2005), spring precipitation (Zhao et al., 2011), summer relative humidity (Saffell et al., 2014), July fog and vapor pressure deficit (Rosso and Hansen, 2003), and March to August temperature (Black et al., 2010). Some research suggests that leaf wetness does not currently limit disease development in most of the coastal Pacific Northwest because there is generally ample moisture for leaf colonization, even in the upper canopy (Lee et al., 2013; Manter et al., 2005; Shaw et al., 2014). However, in drier areas, and during episodic droughts, leaf wetness is likely an important limiting factor, suggesting that climatic controls of this disease vary with geographic location (Lee et al., 2013; Manter et al., 2005).

The relationship of high summer temperatures to Swiss needle cast severity is somewhat unclear. Rosso and Hansen (2003) showed that disease severity decreases at high summer temperatures due to inhibition of fungal development. High continentality (the difference between temperatures of the warmest month and the coldest month) is also associated with decreased disease severity (Zhao et al., 2011). Other research indicates that summer temperature is not strongly linked to pathogen development or disease severity (Manter et al., 2005). Conversely, others suggest that high summer temperatures may be associated with increased disease severity, as indicated by growth impacts shown in dendrochronological records (Black et al., 2010). The uncertainties surrounding the nature of this relationship may be resolved by taking a site-specific approach. Lee et al. (2013) showed that high winter and summer temperatures are associated with increased disease severity at relatively cool and wet sites, whereas high summer temperatures and low summer precipitation are associated with decreased disease severity at relatively hot and dry sites.

Interactions between Swiss needle cast and other biotic disturbance agents have not been well-studied. A single study proposed a negative effect of Swiss needle cast on Douglas-fir beetle susceptibility (Kelsey and Manter, 2004), discussed in further detail below. Interactions among Swiss needle cast, laminated root rot, and black stain root disease and implications for host trees are unknown at this time. However, Swiss needle cast is not a stress-dependent disease, therefore it is unlikely that root diseases predispose hosts to Swiss needle cast.

4.4. Douglas-fir beetle

Douglas-fir beetle is a bark beetle native to the Pacific Northwest that nearly exclusively attacks Douglas-fir (Furniss and Kegley, 2014). Although Douglas-fir beetle is considered the most important bark beetle to this tree species (Furniss and Carolin, 1977), host resistance keeps beetle populations at endemic levels during most periods and small diameter trees are rarely attacked (Furniss and Kegley, 2014; Goheen and Willhite, 2006). Beetles occupy stressed, dying, dead, and recently downed trees during endemic periods; therefore their disturbance impacts are relatively small-scale (Rudinsky, 1966). Disturbance by windthrow is associated with increased Douglas-fir beetle populations in the following year, as the beetle often colonizes recently fallen trees and emerges in the subsequent year (Powers et al., 1999; Rudinsky, 1966). Following emergence, the bark beetle population may attack nearby healthy trees and overwhelm their defenses by mass attack, leading to reduced xylem and phloem transport, and eventual tree mortality, associated with gallery development as well as the introduction of the stain fungus *Ophiostoma pseudotsugae* (Furniss and Kegley, 2014). Under normal climate conditions, the bark beetle population usually declines to an endemic level within several years of an outbreak. However, there have been few reported widespread outbreaks in the Douglas-fir region; the most notable outbreak occurred in the 1950 s as a result of large windthrow events caused by hurricane-force winds in the winters of 1949 and 1950 (Furniss, 2014).

Drought may influence susceptibility to Douglas-fir beetle because the resin flow defense system can be impaired when trees are water-stressed (Rudinsky, 1966). Increased Douglas-fir beetle activity has been noted on south and southwest aspects, though it remains unclear whether this is attributed to increased host moisture stress or increased beetle performance (Powers et al., 1999). However, not all stresses produce physiological responses that attract Douglas-fir beetles. Swiss needle cast-infected trees produce less ethanol as disease severity increases due to carbon starvation, thereby making them less attractive to Douglas-fir beetle (Kelsey and Manter, 2004). However, when Swiss needle cast-infected trees are attacked, those attacks are likely to be successful due to lowered oleoresin defense systems, another symptom of carbon starvation. In addition to the lack of host nutrition due to disease, plantation-aged trees are not ideal for Douglas-fir beetle brood development given their relatively small size (Shaw et al., 2009). However, if another disturbance, such as a windthrow event or episodic drought, causes tree stress or mortality, Swiss needle cast-affected forests could potentially be susceptible to a Douglas-fir beetle outbreak (Kelsey and Manter, 2004).

Interactions with root diseases are extremely important because endemic populations of Douglas-fir beetle depend on stressed and recently fallen trees. Hansen and Goheen (2000) found that approximately 77% of standing Douglas-fir killed by Douglas-fir beetle was located within laminated root rot centers, suggesting that laminated root rot allows the beetle to persist on the landscape in sufficient numbers to respond to windthrow events or drought. Trees infected by *P. sulphurascens* release more ethanol and monoterpenes, compounds that signal host stress, than healthy trees do (Kelsey et al., 2016). This

likely leads to increased attacks, though attacks may only be successful after laminated root rot infection has progressed enough to impair resin flow defense, employed by healthy trees to defend against bark beetle attacks (Kelsey et al., 2016). Black stain root disease infection is also associated with increased ethanol concentrations in Douglas-fir sapwood (Kelsey and Joseph, 1998). It is possible that the same mechanism that signals Douglas-fir beetles to laminated root rot infected trees occurs in black stain root disease infected trees. However, black stain root disease typically occurs in small diameter trees rather than Douglas-fir beetle's preferred size class; other bark beetles like the Douglas-fir pole beetle (*Pseudohylesinus nebulosus* [LeConte]) (Coleoptera: Curculionidae: Scolytinae), may replace Douglas-fir beetle in small diameter black stain root disease-infected trees.

5. Predicted climate change impacts

There are three components of changing climate likely to influence the ecology of the Douglas-fir region: hotter drier summers, warmer wetter winters, and elevated atmospheric CO_2 levels. Climate model simulations suggest that by mid-century the Douglas-fir region will experience hotter drier summers and warmer wetter winters with substantial decreases in snowpack (Mote and Salathé, 2010). Averaged across a number of regionally downscaled climate models, it is predicted that, compared to the 1970–1999 period, the Douglas-fir region will experience increases in annual temperature of 1.1 °C by the 2020 s, 1.8 °C by the 2040 s, and 2.9 °C by the 2080 s (Littell et al., 2009). As of 2014, atmospheric CO_2 concentration levels were ~390 ppm, and are projected to rise to 550–1000 ppm by year 2100 depending on emissions scenario (IPCC, 2014). As current levels are more than 50% higher than pre-industrial levels, climate change impacts in this forest type are likely already occurring. These changes may have direct impacts on tree physiological mechanisms (Table 2), indirectly influence trees by altering the behavior of other disturbance agents, and alter interactions between disturbance agents (Table 3), potentially leading to substantial changes in the disturbance regime.

5.1. Hotter drier summers

Hotter drier summers predicted to occur in the Douglas-fir region as a result of climate change are likely to have substantial impacts on forests. Tree mortality and non-lethal reductions in tree growth that occur as a result of drought and heat events can represent large decreases in net ecosystem productivity (Allen et al., 2015). Both air temperature and soil moisture limit Douglas-fir growth, although the relative influence of each varies somewhat by site conditions (Beedlow et al., 2013). Productivity generally increases until an optimum temperature is reached, which differs with site conditions, at which point it begins to decrease. Optimum temperature and moisture regimes for establishment and growth of a given plant genotype or species can be relatively narrow (Wang et al., 2006). Thus, future climate conditions in the Douglas-fir region may result in reductions in establishment and growth of current local tree populations, increases in competition from genotypes and species better-suited to the new climate conditions, and ultimately, changes in forest composition.

Tree-ring chronologies covering decades to several centuries are key data sources for investigating climate effects on tree growth, but growth-climate relations are difficult to infer because climatic factors are often correlated and interact with each other. Several studies in the western US have found that water supply is often the most limiting factor for tree growth (Littell et al., 2008; Restaino et al., 2016). Across the forest type's moisture gradient, annual radial growth was correlated with water balance, drought, or precipitation during the late summer of the year prior to growth, and during the early summer of the current year of growth (Littell et al., 2008). Restaino et al. (2016) indicate that these forests are sensitive to changes in climatic water deficit and VPD. Vapor pressure deficit scenarios associated with hotter drier summers are strongly linked to decreased productivity, and these scenarios are projected to become dominant throughout the distribution of Douglas-fir by the 2080s.

Other dendrochronological studies in the region indicate that growth responds differently to temperature and precipitation depending upon elevation (Case and Peterson, 2005), topography, and soil characteristics (Brubaker, 1980; Watson and Luckman, 2002). At low to mid-elevations, growth correlates positively with growing season precipitation and soil moisture, and negatively with summer temperatures in both current and prior years (Brubaker, 1980; Case and Peterson, 2005; Watson and Luckman, 2002; Zhang and Hebda, 2004). At high elevations, growth correlates positively with summer and annual temperatures, winter snowpack, and growing season length (Graumlich and Brubaker, 1986; Littell et al., 2008; Nakawatase and Peterson, 2006; Peterson and Peterson, 1994). Therefore, it is probable that at more xeric sites within Douglas-fir region, the influence of heat waves and increased air temperature on the moisture regime will become more limiting as the climate continues to warm, likely leading to decreased productivity on these sites. Productivity may increase at high elevation sites as warming increases growing season length, but the influence of decreased snowpack may confound this effect (Lee et al., 2016).

Fire, characterized primarily by infrequent (on the scale of centuries) high severity wildfire, has played a large role in the disturbance regime in the Douglas-fir region, particularly prior to large-scale fire suppression initiated in the mid-20th century. Area burned is hypothesized by some to increase substantially with hotter drier summers associated with climate change (Littell et al., 2010; Rogers et al., 2011). Although models of area burned are not well-developed for this forest type, retrospective studies of west-side Douglas-fir fire history using fire scars (Weisberg and Swanson, 2003) and sediment records (Long et al., 1998) have noted that past climate patterns have been strongly related to the fire interval in this region. Both soil moisture (Elsner et al., 2010) and fuel moisture (Littell et al., 2010) during the fire season are predicted to decrease with projected climate change, presumably leading to increased area burned. Furthermore, the portions of the region that

Table 2
Major attributes of predicted climate change in the Coastal Pacific Northwest Douglas-fir region, associated factors influencing tree physiology, and direct effects of climate change attributes on tree productivity.

Predicted climate change attribute	Physiological factors	Direct effects
Hotter drier summers: Increased summer temperature Decreased growing season precipitation	Increased vapor pressure deficit; increased respiration in lowland areas; increased length of growing season at higher elevations; reduced photosynthesis; reduced hydraulic conductivity; reduced phloem transport capacity	Reduced growth at low elevations and on xeric sites; possible increased growth at high elevations; increased tree top dieback and mortality at water-limited sites
Warmer wetter winters: Increased winter temperature Reduced winter snow accumulation	Increased winter photosynthesis, altered phenology patterns; possible earlier depletion of available soil water in summer	Increased or decreased bole growth during and following growing season; earlier onset and later cessation of growth
Elevated atmospheric CO_2	Nitrogen limitation; increased water use efficiency and root exudates	Possible increased growth (may be limited by other factors); altered nutrient cycling; effects on insects and diseases largely unknown

Table 3
Major insects and diseases currently important and potentially important in the Douglas-fir disturbance regime with hypothesized responses to climate change.

Biotic agent	Relation to climate change	Hypothesized response to hotter drier summers and warmer wetter winters
Currently important		
Douglas-fir beetle (*Dendroctonus pseudotsugae)*	Associated with windthrow and drought events; response to elevated CO_2 unknown	Increased severity with hotter drier summers and more extreme weather events increasing host stress; improved beetle development with warmer winters possible
Swiss needle cast (*Phaeocryptopus gaeumannii)*	Associated with warm winter temperatures and spring—summer precipitation and leaf wetness; response to elevated CO_2 unknown	Increased severity given warmer wetter winters favoring pathogen development, unclear effect of hotter drier summers, but potential decreased severity; net effect of climate change patterns unknown
Black stain root disease (*Leptographium wagneri)*	Associated with host stress from drought which increases vector attraction, increases host susceptibility to disease; response to elevated CO_2 unknown	Increased severity likely with hotter drier summers increasing host stress, warmer winters favoring improved vector development, although the influence on pathogen virulence is largely unknown; possibility of decreased severity if changing climatic conditions lead to asynchronicity in pathogen and insect development
Laminated root rot (*Phellinus sulphurascens)*	Poorly understood, but not thought to be strongly related to climate; response to elevated CO_2 unknown	Unlikely to change substantially in response to temperature and precipitation
Potentially important under climate change		
Douglas-fir engraver *(Scolytus unispinosus)*	Associated with drought and other biotic stresses	May become more important in west-side Douglas-fir with increased severity and frequency of episodic droughts
Flatheaded fir borer (*Phaenops drummondi)*	Associated with drought or dry, harsh sites	May become more important in west-side Douglas-fir with increased severity and frequency of episodic droughts
Douglas-fir tussock moth (*Orgyia pseudotsugata)*	Poorly understood	May become more important in west-side Douglas-fir with hotter drier summers
Western spruce budworm (*Choristoneura freemani)*	Poorly understood	May become more important in west-side Douglas-fir with hotter drier summers
Armillaria root disease (*Armillaria* sp.)	Warmer, drier conditions may increase tree stress, which is linked to *Armillaria* behavior	As trees become more maladapted, it is anticipated that *Armillaria* will take advantage of stressed and low vigor trees. Warmer winters allow continued development, hotter drier summers increase tree stress

receive relatively low precipitation and experience high summer temperatures experience fire more frequently (Poage et al., 2009). This suggests that hotter drier summers could increase fire frequency throughout the region. However, a recent analysis of projected changes in the Oregon Coast Range's fire regime indicates that although area burned and fire severity may increase slightly under climate change, large wildfires will likely remain rare in this region (Creutzburg et al., 2016). Additionally, it appears that west-side Douglas-fir forests are resilient to a highly variable fire regime as well as variable climatic conditions (Tepley et al., 2014).

5.2. Warmer wetter winters

In the Douglas-fir region, winter temperatures are mild and daytime temperatures below freezing are relatively rare (Waring and Franklin, 1979). Model simulations indicate that up to 50% of the annual net carbon accumulation in this region occurs between October and May, although this is often referred to as the dormant season (Emmingham and Waring, 1977). Along with drier and hotter conditions during the growing season, future climate regimes in the Pacific Northwest are predicted to involve warmer winters with increased precipitation falling as rain, rather than snow (Mote and Salathé, 2010). An increase in winter temperature may extend growing season duration and enhance photosynthesis in the winter in some areas (Creutzburg et al., 2016), particularly at high elevations, but even at these sites the benefits of enhanced photosynthesis in a prolonged growing season could be offset by increases in respiration (Spittlehouse, 2003). Moreover, an earlier start of the growing season may leave less available soil water for the primary growing season in late spring and early summer, resulting in reduced annual carbon uptake (Angert et al., 2005; Hu et al., 2010).

A number of studies have documented significant deviations from historic trends in hydrologic processes in the western U.S. over the last several decades. These include earlier snow melt (Stewart et al., 2005), reduced spring snow water equivalent, defined as the amount of water contained within snowpack (Mote, 2006), and shorter snow accumulation periods (Trujillo and Molotch, 2014). Using a spatially distributed process-based model, Sproles et al. (2013) predicted that a 2 °C increase in mean annual temperature would result in a peak snowpack occurring 12 days earlier and a 56% reduction in basin-wide volumetric snow water storage in the western Cascade Mountains in Oregon. Mote and Salathé (2010) examined simulations from a suite of different models that predicted an average increase in regional winter precipitation of 8% by the 2080s. Although this represents a rise in precipitation, the occurrence of a warmer temperature regime concurrent with the precipitation could result in warm rain that depletes snowpack. In the Douglas-fir region, snowpack represents the dominant storage for water used by forests (Mote, 2006), so climate scenarios that result in reduced winter snowpack are likely to have a substantial impact on soil water content during the growing season.

5.3. Elevated atmospheric CO_2

Elevated atmospheric CO_2 has been hypothesized to elicit a fertilization effect in plants by increasing photosynthesis (Norby et al., 1999) and water use efficiency (Schäfer et al., 2002). Given the fertilization effect, tree productivity is hypothesized to increase, and this effect has been observed in open-air experiments (DeLucia et al., 1999; Norby et al., 1999). However, factors like increased temperature and water stress, changing climatic patterns, and nitrogen availability are all thought to limit tree productivity in the Douglas-fir region (Beedlow et al., 2004). In addition, recent work has noted that cambial activity and xylem formation, processes whose relationships to climate change are poorly understood, are more likely to limit tree productivity than photosynthesis (Rathgeber et al., 2016). Others have emphasized the importance of ectomycorrhizal fungi in the occurrence of a positive fertilization effect under elevated atmospheric CO_2 (Terrer et al., 2016).

Photosynthetic rates increase in Douglas-fir seedlings under elevated atmospheric CO_2 (Lewis et al., 1999, 2001), but the additional carbon does not lead to increased growth (Olszyk et al., 1998a), as the carbon appears to be primarily allocated to soil organic carbon pools (Lin et al. 1999, 2001), rather than to tree biomass production (Olszyk et al., 2003). Total stored soil carbon is unlikely to change significantly under variable atmospheric CO_2, due to decomposition processes in the soil and litter (Beedlow and Tingey, 2007). However, the increased photosynthetic rates observed in seedlings under elevated atmospheric

CO_2 are unlikely to be representative of processes occurring in mature, closed canopy forests (Norby et al., 1999).

Studies on the effects of elevated atmospheric CO_2 have limitations when applied to forested ecosystems. Most studies on this topic are conducted in a greenhouse setting, on seedlings, for only several years. In general, it is unknown whether the trends reported in these kinds of studies will continue as trees mature, or whether the trends are temporary. In addition, effects of elevated atmospheric CO_2 will likely be confounded by the effects of elevated temperatures under real-world climate change conditions. Elevated temperatures have been shown to be associated with bud and needle malformation (Apple et al., 1998), increased stomatal conductance (Apple et al., 2000), and abnormal morphology (Olszyk et al., 1998a, 1998b) in Douglas-fir seedlings. Warming soil temperatures have been shown to increase plant carbon storage by increasing nitrogen availability in a deciduous forest in New England (Melillo et al., 2011), but plant production and nitrogen cycling are limited by soil nitrogen in western conifer forests (LeBauer and Treseder, 2008).

5.4. Interacting effects with climate change

Several climate envelope modeling efforts have indicated that portions of the forested area currently suitable for Douglas-fir will not be suitable under future climate conditions. These effects are predicted to occur primarily at lower latitudes and elevations, while Douglas-fir is predicted to increase at higher elevations and latitudes (Flower et al., 2013; Littell et al., 2010). However, these models use only temperature and precipitation to determine distributions, which represents an oversimplification of the drivers of species range shifts. For example, genetic trials indicate that not all Douglas-fir will respond to climate change uniformly (Bansal et al., 2015a, 2015b; Montwé et al., 2015; St. Clair and Howe, 2007). Therefore, it is unlikely that these models can adequately capture within-species variability. Climate change effects will not be uniform, as competition, stand structure, and forest composition are also predicted to have a large influence on the manifestation of the effects of climate change (Ford et al., 2017). Furthermore, interactions with other biota are not considered in these models and will likely influence tree response to climate change. Climate and disturbance interactions are contingent upon many things, including agent biology (for insects and diseases), host biology, genetics, and disturbance frequency and severity, as well as other components of the physical environment. However, in pathogen epidemiology and insect development models, temperature and moisture are typically key factors, and these factors will change and seasonally shift in projected future climates.

The effects of climate change on laminated root rot are relatively unknown. Some suggest that *P. sulphurascens* may be somewhat resistant to changes in air temperature given the buffering effect of soil (Kliejunas et al., 2009) while others suggest that both the pathogen's spread rate and host susceptibility to disease will increase (Washington State Academy of Sciences, 2013). However, vigor is currently understood to be unrelated to susceptibility to laminated root rot infection (Hansen and Goheen, 2000), so it is unclear whether increased host susceptibility will indeed result from increased host stress anticipated to occur with climate change. It is possible that trees already infected with disease will be more sensitive to hotter drier summers and increased drought stress due to reduced root area and function. This could lead to increased tree mortality and top dieback, and potentially, increased Douglas-fir beetle populations and infestations. However, Armillaria root disease (caused by *Armillaria* species, likely *A. ostoyae* (Romagn.) Herink, Herink, J., in conifers of the Douglas-fir region) is thought to be more responsive to tree stress (Lockman and Kearns, 2016), and it is hypothesized that the disease will become much more important in this region under future climate scenarios (Kliejunas et al., 2009).

Climate change influences on black stain root disease are likely to be complex, given that both a fungal pathogen and several species of insect vectors are involved. Black stain root disease is currently found in a variety of environmental conditions, from hot and dry sites to cool and wet sites (Hessburg et al., 1995), so it is unclear whether climate change will directly affect this disease. If increased frequency or severity of droughts increases host stress, trees may be more vulnerable to attack since these insect vectors respond to ethanol production associated with tree stress. However, there is some indication that cool and moist soil conditions are favorable for pathogen development (Hessburg et al., 1995), so there is a possibility that increased frequency and intensity of droughts could lead to a decline in pathogen virulence.

The intensification of short-rotation monoculture Douglas-fir forests, particularly on industrial land, will continue to provide attractive substrate, in the form of recently created stumps, for insect vector feeding and reproduction. Therefore, the potential for increase in black stain root disease in planted forest landscapes under drought or other stress, coupled with intensification of management, will be significant. However, increased temperatures could also alter insect life cycles, leading to potential asynchronicity with *L. wageneri*, and a lowered pathogen vectoring ability. Furthermore, the interactions may change in different ways for each insect vector species.

Direct impacts on Swiss needle cast due to climate change are likely to be site-dependent (Lee et al., 2013) and to depend on the specifics of the climate change scenario. Many climate change predictions indicate that conditions will become warmer year-round and that droughts will be more frequent. Dry and hot conditions are hypothesized to be inhibitory to fungal development (Rosso and Hansen, 2003), especially on xeric sites (Lee et al., 2013). These conditions are predicted to lead to decreased disease severity (Zhao et al., 2011). Conversely, synchronous outbreaks of Swiss needle cast noted across western Oregon have been found to exacerbate the negative growth impacts from high VPD (Lee et al., 2013, 2016), suggesting the potential for increased disease severity during hot and dry periods. However, if warm spring temperatures co-occur with rain events prior to onset of drought, conditions for inoculum production would be ideal, and would likely lead to increased disease. While there has been a 33% decline in summer coastal fog frequency since the mid-20th century that is likely to continue under climate change (Johnstone and Dawson, 2010), recent trends in the Douglas-fir region have shown increased water availability in May and June (Mildrexler et al., 2016). This trend may explain increasing intensification of the disease in the past decade (Ritóková et al., 2016). Given that the *P. gaeumannii* development-limiting threshold of 110 mm of June-July precipitation (Hood, 1982) continues to be met, it is likely that Swiss needle cast will continue to be an important disease in Douglas-fir region.

The interacting effects of warmer wetter winters, hotter drier summers, and biotic disturbance agents such as Swiss needle cast are likely to have direct and indirect effects on the Douglas-fir beetle. Douglas-fir beetle experiences an obligatory adult diapause during the winter (Ryan, 1959), which could be disrupted if minimum winter temperatures rise beyond a certain level, potentially leading to decreases in beetle fitness (Bentz et al., 2010). The Douglas-fir beetle currently has a one-year life cycle in which multiple broods emerge at various times of the year (Furniss and Kegley, 2014). It is unknown whether climate change will have an effect on the Douglas-fir beetle life cycle or timing of brood emergence. However, host susceptibility and attractiveness is negatively influenced by severe Swiss needle cast (Kelsey and Manter, 2004), so in severely diseased stands, Douglas-fir beetle may not be able to react to typical climate drivers.

The most prevalent indirect climate effects on Douglas-fir beetle are those of increased risk of widespread windthrow due to more extreme weather events (Elsner et al., 2008; Emanuel, 2005) and increased host stress under warmer temperatures and more frequent drought (Ayres, 1993). Downed trees emit ethanol, while drought and temperature-stressed Douglas-fir both emit ethanol and have lowered oleoresin defenses (Rudinsky, 1966), therefore Douglas-fir beetle attack success during the endemic phase may increase with climate change. Higher

success rates during endemic phases may also result in higher probability of epidemic initiation. It should be noted, however, that several studies have shown wide genetic variation in traits like drought tolerance and cold hardiness in Douglas-fir, suggesting that even within a single species and region, these interactions will not be uniform (Bansal et al., 2015a, 2015b; St Clair and Howe, 2007).

Forest management is commonly suggested as a means to mitigate the impacts of climate change on forest ecosystems. In particular, reduction of density via forest thinning is often proposed as a management option to improve drought resistance and increase tree vigor (Bradford and Bell, 2017; D'Amato et al., 2013). Although this strategy is implemented more frequently in dry forests, it is currently a popular approach for increasing structural diversity in the Douglas-fir region (Kuehne et al., 2015). However, the effectiveness of this strategy is not always straightforward, and results can vary with silvicultural prescription, stand age and type, as well as other site characteristics (Sohn et al., 2016). Furthermore, the major biotic disturbance agents in the region may respond differently to various forest management practices, which could lead to variable results in terms of overall forest health. These agents also interact with one another, making for complex long-term interactions surrounded by many uncertainties following forest management actions.

6. Knowledge gaps

Regardless of climate change scenarios, the biotic disturbance agents discussed above are likely to remain prominent or increase on the landscape. However, significant questions remain regarding interactions of trees, climate, and disturbance factors. We outline key areas in which further study is needed below.

6.1. How do biotic disturbance agents influence the fire regime in the Douglas-fir region, and how will these interactions change with global climate change?

Given the trends of hotter drier summers, and warmer wetter winters expected in Douglas-fir region, fire frequency is likely to increase as favorable conditions for fire initiation will become increasingly common (Abatzoglou and Williams, 2016). Additionally, there is a potential for warmer wetter winters to be associated with increased productivity, leading to increased biomass and fuel loads. Fuel loads and canopy connectivity in natural stands are generally high and should favor large extent, high intensity fires, while fire behavior in young plantations is not well-understood. Dramatic changes to the fire regime may also result in a forest type conversion in some areas of the Douglas-fir region. Conversely, in other areas increased fire frequency may facilitate increased Douglas-fir dominance over fire-sensitive species like western hemlock.

Interactions between fire and biotic disturbance agents such as Douglas-fir beetle, Swiss needle cast, laminated root rot, and black stain root disease are poorly understood. These disturbance agents may influence fuel dynamics and fire behavior in various ways. Conversely, fire damage may influence host response or susceptibility to any of these agents. For example, Furniss and Carolin (1977) note that Douglas-fir beetles tend to increase in response to fire, drought, and windthrown mature timber. Quantifying these interactions will become increasingly important as fire is predicted to become more prevalent in Douglas-fir forests with climate change (Littell et al., 2010).

Interactions will differ among disturbance agents leading to more specific questions such as: Do increased terpenes associated with Douglas-fir beetle attacks lead to attacked trees becoming more flammable? Do decreased bole water content and foliar moisture content associated with drought-stress increase tree flammability? How many drought-stressed or Douglas-fir beetle-attacked trees would need to be present and simultaneously in the "red stage" (i.e., immediately following attack, with an intact canopy, low foliar moisture, high terpene concentration) to create a biologically significant impact on fire behavior? Does the reduction in foliage associated with Swiss needle cast lead to decreased canopy bulk density and decreased likelihood of crown fire? Does Swiss needle cast have an effect on foliar moisture content, and therefore, foliage flammability? Do discontinuous fuel beds created by root diseases and windthrow result in significant changes to fire behavior?

6.2. Will climate change lead to amplification of existing biotic disturbance agents or expansions of agents currently common in dry mixed-conifer forests of the Douglas-fir region?

While the introductions of alien pests and diseases are a persistent threat in this region, particularly given that it is dominated by a single species (Franklin et al., 2017), changes in climate present the possibility of amplification of impacts of biotic disturbance agents that are not currently of high importance (Table 3). The Douglas-fir beetle is thought to behave differently in dry forests with outbreaks lasting longer and killing more trees than is typical for the west side Douglas-fir region (Furniss, 2014; Furniss and Carolin, 1977; Goheen and Willhite, 2006). Given a warming climate, it is unknown whether the behavior of the Douglas-fir beetle will change in the west side Douglas-fir region. The Douglas-fir engraver (*Scolytus unispinosus* LeConte), Douglas-fir pole beetle (*Pseudohylesinus nebulosus* LeConte) (Coleoptera: Curculionidae), and flatheaded fir borer (*Phaenops drummondi* [Kirby]) (Coleoptera: Buprestidae) are typically secondary disturbance agents and often cause the most damage during droughty periods (Goheen and Willhite, 2006; McMullen and Atkins, 1962). Although relatively little is known about these insects' potential to cause increased tree mortality in the Douglas-fir region, it is possible that their impacts will become more significant in this region as summers become hotter and drier and drought stress increases.

Two defoliating insects, Douglas-fir tussock moth (*Orgyia pseudotsugata* [McDunn.]) (Lepidoptera: Lymantridae) and western spruce budworm (*Choristoneura freemani* [Clemens]) (Lepidoptera: Tortricidae), currently cause minor and infrequent disturbance in the Douglas-fir region, but commonly outbreak in interior Douglas-fir in Washington and Oregon (Goheen and Willhite, 2006). Predicted decreases in water availability and increased temperatures (Abatzoglou et al., 2014) could lead to an increase in habitat that is more similar to interior Douglas-fir forests and a greater tree susceptibility to insect defoliators. Spatiotemporal patterns of western spruce budworm outbreaks in interior British Columbia are driven by localized outbreaks during periods of regional-scale low autumn precipitation, followed by an outward expansion from infestation centers throughout the region (Senf et al., 2016). Regional patterns of projected moisture deficits will likely increase the susceptibility of forests in the Douglas-fir region to localized outbreaks and possible expansion regionally. However, further research is needed to understand the relationships between these insects and climate, as well as other factors that might influence their amplified activity in the interior Pacific Northwest as compared with the Douglas-fir region, such as forest structure and composition, host genetics, and interactions with other disturbances.

Climate change response of pathogens commonly found in old growth Douglas-fir forests rather than in young forests is largely unknown. For example, little formal research has been conducted regarding the impacts of *Phaeolus schweinitzii* in the region, yet it is an important butt rot of older trees associated with lower stem breakage and tree blowdown (Goheen and Willhite, 2006). We are not aware of any research indicating that tree stress is a factor in *P. schweinitzii* ecology. Furthermore, two pathogens of potential importance, *Phytophthora pluvialis* Reeser, Sutton, & Hansen and *Rhizoctonia* spp. have been recently noted to cause localized defoliation to hemlock and Douglas-fir in the region (Everett Hansen, personal communication). It is currently unclear whether the damage caused by these pathogens will be sustained over many seasons, or if it is an ephemeral event. Links to

climatic events like episodic drought, warmer winters, or a chronically drier climate, are also not yet understood, but may play a role in the severity of disease caused by these pathogens. Research is needed to understand these interactions, but biotic disturbance agents potentially influenced by climate change must be considered when projecting alterations to the overall disturbance ecology of these forests.

The effect of elevated atmospheric CO_2 on biotic disturbance agents in the Douglas-fir region is poorly understood. Experimental studies have shown that Douglas-fir increases photosynthesis under elevated CO_2 but the carbon appears to be primarily allocated to soil organic carbon pools (Lin et al., 1999, 2001). Further, mycorrhizal associations have been shown to control CO_2 fertilization under nitrogen limitation, particularly in trees (Terrer et al., 2016). Because elevated atmospheric CO_2 could affect both carbon assimilation and allocation, both insect pests and fungal pathogens could be affected by changes in the quantity and quality of nonstructural carbohydrates in various tissues, and by increased carbon allocation belowground and the consequent changes to the rhizosphere, respectively. Research is needed to identify potential amplification of insects and diseases from elevated atmospheric CO_2 in the region.

6.3. How does the interaction between climate and the disturbance regime influence ecosystem functioning and services? How will these change with altered disturbance regimes that are expected in the future?

Forested ecosystems provide critical ecosystem services such as carbon sequestration, maintenance of water quality and air quality, and habitat for wildlife (Curtis and Carey, 1996; Harmon et al., 2004; Kline et al., 2016; Ruggiero et al., 1991). Native forest insects and diseases, although potentially destructive to wood volume production, play an important role in ecosystem processes, including nutrient cycling and carbon sequestration, and may provide other ecosystem services, such as a positive influence on biodiversity, creating dead trees, partially dead trees, and snags for wildlife, and increasing heterogeneity on the landscape. Changes in effects from biotic disturbance agents resulting from changing climate may also negatively influence ecosystem functioning and ecosystem services with alteration of carbon and nutrient cycling, reduction in species diversity, high densities of tree mortality, and reduction of wildlife habitat and food sources (Weed et al., 2013).

While we have focused on interactions affecting existing Douglas-fir, altered disturbance regimes will likely impact co-existing tree species, forest regeneration and, consequently, the nature of future forests (Peterson et al., 2014). Little is known about how biotic interactions with climate change will affect reproduction of other important tree species during or after disturbance in the Douglas-fir region. Specific questions that must be addressed include: Will native forest insect species begin to behave like invasive species as the climate continues to change? Are non-native invasive species likely to play a bigger role in the region in the future? Will altered importance of predominant biotic disturbance agents affect ecosystem processes such as carbon sequestration and nutrient cycling? Will ecosystem services be affected? Are we over-predicting ecosystem services that our forested landscapes can provide?

Long-term research on the effects of forest harvesting on ecosystem functions under various active management practices and changing climate are largely unknown. Various harvesting systems (i.e., ground based vs. cable logging) are used depending on the landowner and terrain, which may have variable influences on water quality, soil erosion, site productivity, and stand susceptibility to insects and pathogens (Dyck et al., 1994; Kellogg et al., 2002). Regardless of the system, impacts of logging on site productivity are thought to be relatively minimal, particularly in areas with high levels of soil organic matter and substantial precipitation infiltration, which aids in minimizing soil erosion (Kellogg et al., 2002). However, further research is needed to determine whether these trends will remain into the future.

7. Conclusions

The disturbance regime in Douglas-fir region consists of generally long-term fire return intervals interacting with biotic and abiotic factors, which then interact with the anthropogenic disturbance of forest management. Generalizations beyond the region are limited due to the unique aspects of abiotic and biotic disturbance agents in these Douglas-fir forests. Because climate-disturbance interactions vary depending on topographic and edaphic conditions, management actions should be tailored to specific forest types and locations. Impacts of individual insect and disease agents in the Douglas-fir region are relatively well-understood, but their effects have not, in general, been included in quantitative models. Furthermore, knowledge of the interactions among disturbance agents is generally lacking and the uncertainties surrounding the ways in which climate change impacts will manifest in the Douglas-fir region lead to uncertainty regarding the future changes to the disturbance regime. However, the influence of biotic disturbance agents in this forest type is substantial. It is imperative to include biotic and abiotic disturbance effects, in addition to constraints of temperature and moisture, in models of forested ecosystems to accurately capture forest dynamics and understand how forests may change in the future. Ultimately, this information is needed to inform management actions. Adaptive forest management strategies to changing climate for the broader Pacific Northwest, USA region, emphasize preserving species diversity by creating refugia and migration corridors, and include stand thinning, assisted migration, and genetic resistance (Franklin et al., 1991; Spies et al., 2010). To be effective in specific forest types, such as those in the Douglas-fir region, adaptive management must consider changing disturbance regimes and interactions between biotic and abiotic factors.

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